

## COMPARISON BETWEEN PLANT SPECIES IN BUSHY-TAILED WOODRAT MIDDENS AND IN THE HABITAT

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**ABSTRACT.**—Bushy-tailed woodrats (*Neotoma cinerea*) collect vegetation and store it in middens. We asked to what extent plant species collected by woodrats reflect the array of species growing in the habitat. Species composition of plant clippings at 20 bushy-tailed woodrat middens in central Colorado was compared to vegetation growing within 30 m of the dens. Amount of overlap between midden and habitat species was low (25–49% when all taxa were included; however, if only woody taxa were considered, overlap was 71–89%). Sorensen's Index of Similarity exhibited a like pattern; the index increased markedly if only woody taxa were included. Only one plant species not found within 30 m of a den occurred in significant amounts in the middens. Bushy-tailed woodrats collected a wide array of species but were more selective the greater the habitat plant diversity. Results of this and other studies indicate that the concordance between midden contents and habitat vegetation decreases with increasing habitat plant diversity. Ancient woodrat middens are nonetheless useful to paleontologists seeking to reconstruct past vegetation associations since woody vegetation is well represented in middens.

*Key words:* bushy-tailed woodrat, *Neotoma cinerea*, midden, foraging, paleoecology, fossil midden.

The bushy-tailed woodrat, *Neotoma cinerea*, occurs in western North America in a wide range of habitats and temperature regimes. In Colorado, *N. cinerea* most often lives in shrub and woodland communities where Douglas fir, ponderosa pine, aspen, and a variety of shrubs such as sagebrush, snowberry, rabbitbrush, and scrub oak occur. However, the bushy-tailed woodrat is more dependent on the existence of suitable crevices in cliff outcrops than on the type of vegetational association (Finley 1958). The woodrat constructs its nest in such a crevice, wherein it typically accumulates a separate midden consisting chiefly of bones, fecal pellets, woody branches, and plant clippings. Separate food caches may be nearby. Clippings consist of either vegetation stored for future consumption or debris remaining after partial consumption by a woodrat at the den.

We investigated species composition of plants collected by bushy-tailed woodrats in Colorado at elevations of 2400 and 2530 m. Sites included different vegetational associations ranging from xeric to dry-mesic. The occurrence of individual plant species in middens, nests, and food caches was compared to the presence of each species growing within 30 m of the cliff. This comparison is of interest for several reasons. First, paleontologists use

contents of fossil woodrat middens to determine species composition of Pleistocene and early Holocene vegetational communities (Betancourt et al. 1990). It is therefore important to know whether woodrats collect plant material based on availability (cf. Wells 1976), or whether woodrat selectivity introduces a significant bias in species composition of midden deposits (cf. Dial and Czaplewski 1990). Second, little is known about the behavioral ecology of bushy-tailed woodrats. Analysis of these midden contents provides information on the foraging and collecting behavior of *N. cinerea* in habitats differing in plant diversity and species composition. Third, midden contents may mirror woodrat diets. Dial (1988), in a study of *N. albigula*, *N. devia*, and *N. stephensi* in a shrub-steppe/juniper woodland ecotone, determined that plant clippings at middens did reflect the diet of those woodrat species, although the two were not strongly correlated.

We asked the following question: To what extent do the species collected by bushy-tailed woodrats and deposited in the den area represent the availability of plant species in the habitat? Our results also provided information on distances traveled by foraging bushy-tailed woodrats. Diet per se will not be discussed here.

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## STUDY AREA

Three sites in Gunnison County, Colorado, were studied. Robert B. Finley conducted woodrat studies at these cliffs nearly 40 years ago (Finley 1958). Finley IA and Finley IB are different walls of a rock outcrop that forms a small canyon. The canyon is located 4.5 km north of Almont on the east side of Colorado State Highway 135 at an elevation of 2530 m. Finley IA has a western exposure and IB faces south. The cliffs are composed of sandstone with granite caps. The nearly level cliff top is sparsely vegetated compared to the area below the cliffs. Spruce (*Picea pungens*) and aspen (*Populus tremuloides*) are common below Finley IA cliff, and the area at the base of Finley IB cliff is a sagebrush and mixed-shrub community with few trees.

The third site, Finley II, is 1.7 km south of Almont along Highway 135 at an elevation of 2400 m. The cliff has an eastern exposure and, like Finley I, is sandstone. Finley II is in a juniper/sagebrush community that includes yucca, cactus, and a variety of shrub species. The vegetation on top of and below the cliff is similar. Finley II is the most xeric of the three sites.

These sites were chosen because they differed in vegetational composition and because live-trapping confirmed the presence of resident *N. cinerea* populations.

## METHODS

Bushy-tailed woodrats do not live in middens themselves, and the study site middens tended to be diffuse and shallow, and were unindurated; food caches were small, discrete piles on rock or sandy soil. From 1 July through 15 August 1986, all plant clippings found on the surface of middens, in nearby food caches, and in the nests (not including the nest material) were identified. In all but a few instances identification of plant fragments was possible at the site. For brevity, we will refer to all clippings from middens, caches, and nests as being from middens. Fragments from 20 middens were examined.

We were unwilling to permanently remove den material for sifting or sorting due to an ongoing woodrat behavior study. This may have introduced a source of bias, since small (<5 mm in length) plant fragments may have

fallen into the loose debris pile of a midden and not been recorded. However, virtually all fragments in food caches and nests were accessible, and some seeds and fine material were recovered from middens with our protocol.

Vegetation near the cliffs was sampled during the second and third weeks of August and was divided into three categories: (1) herbaceous plants, including cacti; (2) shrubs; (3) trees, including saplings (diameter at breast height <2.5 cm). Botanical nomenclature follows that of Weber (1976) and Barrell (1969).

All trees and shrubs within 30 m of the cliff face at each site were included. Tree basal area and shrub canopy were calculated. Herbaceous species within 30 m of the cliff edge were sampled using 0.1-m<sup>2</sup> quadrats that were placed by drawing numbers randomly and pacing off the appropriate distances. The minimum number of quadrats needed to adequately survey the community was determined by constructing a species-area curve. Individual plants were counted except for clonal species such as the grasses and *Antennaria*, *Arctostaphylos*, and *Selaginella*, for which the percentage of groundcover was estimated. All species recorded in the middens and the habitat are listed in Appendix 1 and 2.

## RESULTS

One measure of concordance between midden contents and species in the habitat is the percentage of taxa they have in common. When vegetation was divided into categories of woody (trees, shrubs) and herbaceous (forbs, grasses) species, shared taxa ranged from 0 to 100% (Table 1). Woody species in the habitat were better represented in middens than were herbaceous species, and at two sites there was a greater overlap among trees than among shrubs (Table 1).

When all taxa were pooled, overlap at the three sites ranged from 27.8% at Finley IA to 48.5% at Finley II (Table 2). Removing grasses from the calculation increased the percent overlap, and when only woody species were included, overlap increased markedly at all sites (Table 2).

Sorensen's Index is commonly used to assess similarities between plants in woodrat middens and in the environment (Spaulding

TABLE 1. Number of plant taxa in the middens (numerator) versus the number of plant taxa in the habitat (denominator). Percent of shared taxa outside parentheses. N = number of middens examined.

	Trees	Shrubs	Forbs	Grasses
Finley IA N = 6	75% (3/4)	75% (6/8)	20% (6/31) <sup>a</sup>	0% (0/12)
Finley IB N = 7	100% (3/3) <sup>a</sup>	64% (9/14)	36% (11/31) <sup>a</sup>	18% (2/11)
Finley II N = 7	100% (2/2)	86% (6/7) <sup>a</sup>	25% (4/16)	50% (4/8)

<sup>a</sup>One species in midden not found growing within 30 m of the cliff base. That species not included in the numerator.

et al. 1990). SI values were relatively low; if only woody species were considered, the similarity index was 80% or greater (Table 2). Regardless of which categories of plants were included in the calculation, the greater the number of taxa present, the lower the similarity index.

DISCUSSION

In the years since Wells (1976) proposed a connection between the wealth of plant macrofossils preserved in middens deposited by long-dead woodrats and ancient plant communities, many paleontologists have used fossil woodrat middens to reconstruct Pleistocene and Holocene vegetational associations and corresponding climates (e.g., Cole 1983, Cole and Webb 1985, Spaulding 1985). The validity of these reconstructions rests in large part upon the extent to which *Neotoma* middens contain an accurate representation of the surrounding vegetation.

The amount of overlap between taxa collected by *N. cinerea* and taxa growing in the vicinity (Table 2) was considerably lower than in other studies. Spaulding (1985) reported a 68–84% overlap for taxa growing within 30 m of an unspecified woodrat species' middens. Dial and Czaplewski (1990) indicated an average of 71.8% overlap for *N. albigula*, 45.8% for *N. devia*, and 53% for *N. stephensi*. If, for each of our sites, taxa that were uncommon and of low biomass in the habitat and taxa that appeared in only one midden and in low abundance were omitted from analysis, then overlap for Finley IA was 40%, Finley IB 53%, and Finley II 64%. Omitting rare taxa increases the degree of overlap, but still far fewer than three-quarters of the common plants in the vicinity appeared in the midden.

An average of 25% of all species present in *N. cinerea* middens were herbaceous (range

for the three sites, 13.9–32.0%). There were few herbaceous perennials in the areas sampled by Spaulding (1985) and Dial and Czaplewski (1990). If herbaceous perennials are omitted from our *N. cinerea* data, the overlap increases from an average of 39.6% for all sites to an average of 78.2%. This latter percentage is comparable to Spaulding's results (1985) and those for *N. albigula* (Dial and Czaplewski 1990).

Other workers assessed the similarity between midden plant taxa and habitat plant taxa with Sorensen's Index. These similarity indices generally were greater than the 43–63% obtained from our *N. cinerea* data. Published similarity indices were 67–84% (Spaulding 1985), 80% (Cole and Webb 1985), 89% (Cole 1983), and 64–92% (Cole 1982) for unnamed *Neotoma*. Vaughan (1990) reported lower similarity indices and listed approximate values of 50% for *N. mexicana* and 30–40% for *N. lepida*, *N. albigula*, *N. stephensi*, and *N. devia*. If only woody taxa from the *N. cinerea* data are included, the range for the index is 80–89% (Table 2).

TABLE 2. (A) Percent of overlap between plant taxa present in middens and those present in habitat. (B) Similarity between plant taxa present in middens and those present in habitat as calculated with Sorensen's Index.  $SI = 2C/A + B$  where A = number of species in middens, B = number of species in habitat, and C = number of species in both middens and habitat. Total number of taxa in habitat: Finley IA, 54; Finley IB, 59; Finley II, 33.

	All taxa	Grasses omitted	Woody taxa
(A)			
Finley IA	27.8	35.7	75.0
Finley IB	42.4	47.9	70.6
Finley II	48.5	48.0	88.9
(B)			
Finley IA	42.9	50.8	85.7
Finley IB	58.1	60.5	80.0
Finley II	62.7	63.2	88.8

What conclusions can be reached from inspection of these data on different *Neotoma* species living in various vegetational communities? How accurately can the habitat vegetation be predicted by analysis of woodrat middens?

It should be noted that typical paleomiddens differ from the modern middens analyzed in this study. Nonindurated modern middens represent a shorter collection period than do ancient indurated ones. We have no way of assessing whether plant clippings we identified are an accurate sample of plant debris that would accumulate during several years. Relatively low frequency of grasses and forbs in *N. cinerea* middens could be a result of our overlooking small plant fragments that would be recovered in the sieving procedure used on paleomiddens. However, Dial and Czaplewski (1990) did not identify plant parts <3 mm in diameter; yet they reported an average overlap of 72% between modern middens of *N. albigula* and adjacent vegetation. And, as stated earlier, we did identify some small plant fragments in our middens, so a strong bias against grasses and forbs as a result of not including fine material does not alone explain the low overlap between these types of plants in the middens and in the habitat.

Plant species richness in the *N. cinerea* habitat was considerably greater ( $N = 33\text{--}59$ ) than at other sites. For example, at Spaulding's (1955) sites, there were 14–19 taxa; Dial and Czaplewski's (1990) transects included 20 species plus several grasses. When the results of all studies were compiled, Sorensen's Index was, in general, negatively correlated with species diversity—the greater the habitat diversity, the lower the degree of concordance between midden contents and habitat. In diverse habitats then, the predictability of habitat vegetation from midden contents is reduced.

Different woodrat species exhibit different degrees of selectivity during collecting (Dial and Czaplewski 1990, Vaughan 1990). Dial's (1954) removal experiment showed that midden contents changed, sometimes drastically, following a change in the species of the den occupant. *N. cinerea* and *N. mexicana* are considered generalist collectors (Finley 1955, Vaughan 1990), whereas *N. stephensi* is a specialist and unquestionably its middens offer a

strongly biased account of the vegetational community (Vaughan 1952). However, our *N. cinerea* data indicated that although *N. cinerea* midden contents include many plant species, less than 50% of the species within 30 m of the midden are represented. When considering all plant taxa, our *N. cinerea* middens are not very good predictors of the habitat vegetation. This is true in habitats of different levels of diversity, even though *cinerea* is among the most catholic collectors within the genus. In fact, bushy-tailed woodrats are more selective the greater the vegetational diversity.

If, however, paleontologists are primarily concerned with community type rather than specific floral components, woodrat middens probably are good predictors. There is strong concordance between the woody species collected by woodrats and the woody species found in the environment. Since communities with woody flora can be characterized in large part by which woody species are present (e.g., Engelmann spruce/subalpine fir forest vs. ponderosa pine forest), community type and associated climate can be ascertained using midden contents, as long as the species responsible for the midden is not one whose extreme selectivity introduces substantial bias.

Individual *N. cinerea* had home ranges much larger than 60 m in diameter (Fraser unpublished data), but only three plant species present in middens did not grow within 30 m of the cliff edge. *Cirsium undulatum*, present in only small amounts in only one midden at each site, grew within 40 m of the cliff edge. A bit of *Juniperus scopulorum* was present in one midden at Finley IB. The only taxon that appeared in significant amounts in middens despite its absence close to the cliff was *Eurotia lanata*, winterfat, at Finley II. Winterfat was quite common 50 m and more from the base of the cliff. Thus, with one exception, our bushy-tailed woodrats need not travel more than 30 m from home to forage.

In general, most species of woodrats do not travel very far to forage (summarized in Finley 1990), and the bushy-tailed woodrats in this study conformed to that pattern. It is largely assumed that this behavior greatly reduces the risk of predation. Results of our midden analysis present an intriguing ques-



tion we are currently investigating: If woodrats at our sites can satisfy their foraging needs within a 30-m radius of their dens, and if it is risky to travel away from the shelter of the cliff, then why, even outside of breeding season, do individuals regularly travel distances of 100–500 m from their dens?

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APPENDIX 1. Plant species found in bushy-tailed woodrat middens and habitat. M indicates present in midden, H indicates present in habitat

	Finley 1A	Finley 1B	Finley 1H
TREES			
<i>Juniperus scopulorum</i>	H	M	M H
<i>Picea pungens</i>	M H	M H	—
<i>Pinus ponderosa</i>	M H	M H	—
<i>Populus tremuloides</i>	M H	M H	—
<i>Pseudotsuga menziesii</i>	—	—	M H
SHRUBS			
<i>Amelanchier alnifolia</i>	—	H	M H
<i>Artemisia tridentata</i>	M H	M H	M H
<i>Chrysothamnus</i> <i>nauseosus</i>	—	M H	—
<i>C. parryi</i>	H	M H	—
<i>C. viscidiflorus</i>	H	H	M H
<i>Eurotia lanata</i>	—	—	M
<i>Holodiscus dumosus</i>	—	M H	—
<i>Juniperus communis</i>	M H	M H	—
<i>Pentstemon</i> <i>floribunda</i>	—	H	—
<i>Purshia tridentata</i>	M H	M H	—
<i>Ribes cereum</i>	M H	M H	—
<i>Rosa woodsii</i>	M H	M H	—
<i>Rubus idaeus</i>	—	M H	—
<i>Symphoricarpos</i> <i>lecontei</i>	M H	H	M H
<i>Tetradymia canescens</i>	—	—	M H
<i>Yucca glauca</i>	—	—	M H

	Finley IA	Finley IB	Finley II
<b>Forbs</b>			
<i>Anemone patens</i>	H	M.H	H
<i>Arnica montana</i>	H	M.H	H
<i>Antennaria dioica</i>	H	M.H	—
<i>Artemisia tridentata</i>	M.H	M.H	—
<i>A. frigida</i>	M.H	M.H	M.H
<i>Ceanothus velutinus</i>	M	M	M.H
<i>Hebe pinnatifida</i>	M.H	M.H	—
<i>Hesperis matronalis</i>	H	M.H	—
<i>Lupinus albus</i>	—	M.H	—
<i>Geranium macranthum</i>	—	M.H	—
<i>Opuntia polyacantha</i>	—	—	M.H
<i>Sedum spectabile</i>	—	—	M.H
<i>Smilacina stellata</i>	M.H	—	—
<i>Solidago missouriensis</i>	M.H	M.H	—

<b>GRASSES</b>			
<i>Adiantum</i> sp.	—	H	M.H
<i>Festuca arvensis</i>	H	H	M.H
<i>Muhlenbergia</i> sp.	H	M.H	H
<i>Oryzopsis hymenoides</i>	—	H	M.H
<i>Elyx</i> sp.	H	M.H	M

APPENDIX 2. Plant species present in the habitat of bushy-tailed woodrats, but not present in middens. H indicates present in habitat.

	Finley IA	Finley IB	Finley II
<b>SHRUBS</b>			
<i>Rhus trilobata</i>	—	H	H
<b>Forbs</b>			
<i>Achillea lanulosa</i>	H	H	—
<i>Agrostis tenuifolia</i>	—	H	H
<i>Androsace</i>	—	—	—
<i>Asplenium</i>	H	—	—
<i>Androsace</i>	H	—	—

	Finley IA	Finley IB	Finley II
<i>Artemisia tridentata</i>	H	H	—
<i>Argemone arvensis</i>	—	H	—
<i>Artemisia ludoviciana</i>	—	—	H
<i>Bahia dissecta</i>	H	—	—
<i>Cassiope linearifolia</i>	H	H	H
<i>Chaenactis douglasii</i>	H	H	—
<i>Chenopodium album</i>	H	H	H
<i>Cryptantha crataegi</i>	H	H	—
<i>Dasycarpus</i> sp.	H	—	—
<i>Dianthus deltoides</i>	H	H	—
<i>Eriogonum punctatum</i>	H	H	—
<i>E. spectabile</i>	H	H	—
<i>Eriogonum cernuum</i>	—	H	H
<i>E. racemosum</i>	—	—	H
<i>E. subulatum</i>	—	H	—
<i>E. umbellatum</i>	—	H	—
<i>Galium boreale</i>	H	—	—
<i>Isomopsis aggregata</i>	—	—	H
<i>Lupinus albus</i>	H	—	—
<i>Mahonia repens</i>	H	H	H
<i>Mammillaria crinita</i>	—	H	—
<i>Oenothera lutea</i>	H	—	—
<i>Physalis vitifera</i>	—	—	H
<i>Phlox paniculata</i>	H	H	—
<i>Sedum lanceolatum</i>	—	H	—
<i>Silene acaulis</i>	H	H	—
<i>Senecio jacobinae</i>	H	H	H
<i>Tanacetum officinale</i>	H	H	—

<b>GRASSES</b>			
<i>Blechnum sp.</i>	H	H	H
<i>Bouteloua curtipendula</i>	H	H	H
<i>Bromus</i> sp.	H	H	H
<i>Carex</i> sp.	H	—	H
<i>Elymus canadensis</i>	H	—	—
<i>Hesperis matronalis</i>	H	—	—
<i>Koeleria cristata</i>	H	H	—
<i>Phlox</i> sp.	H	H	—
<i>Scirpus americanus</i>	H	H	—